TEMPLATES FOR THE ORGANIZATION OF SOIL ANIMAL COMMUNITIES IN TROPICAL FORESTS

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Abstract. **-** This paper presents a review on the results of decomposition and animal community studies carried out in tropical and temperate forests and also discuss the importance of such food habitat templates for the organization of soil animal communities. The forest functioning determines the abundances of Collembola through the litterfall and decomposition rates. The abundances of Collembola were determined by the amount of habitats, i.e. soil organic layer and ranged from 10^3 to 10^4 per 1 m^{2}·. Decomposition processes are different between the temperate and tropical forests, not only in the decomposition rates but also, the carbon and nitrogen dynamics. These decomposition processes are well related to the feeding group of collembolan species. The tropical forests are characterized by the diversity of fungivorous collembolan species and low abundances of saprophagous species.

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INTRODUCTION

The functioning and structure of terrestrial ecosystems are shaped and maintained by the plant-decomposer interactions. The food and habitat of animal populations are biogenic and mainly of plant origin in terrestrial ecosystems (Takeda, 1995a). In terrestrial ecosystems, organic matter is accumulated as plant and soil organic biomass which provide the food and habitat for animal populations. In soil sub-systems, the food-habitat templates are provided mainly by plant litter such as leaves, branches and fallen logs. The structure and composition of litter is modified through the decomposition processes. Decomposing litter provides foods and microhabitats for the organization of soil animal communities (Takeda, 1987).

The results of decomposition and animal community studies carried out in tropical forests and the importance of such food habitat templates for the organization of soil animal communities are presented in the following sections.

THE FUNCTIONING OF TROPICAL FOREST ECOSYSTEMS

The functioning of tropical forest ecosystems have been compared with those of temperate forests and are characterized by the high primary production and the rapid decomposition rates of organic matter. In forest ecosystems, litterfall is an important flux of carbon (energy) and nutrients into the soil decomposer systems where nutrients are mineralized for plant growth. The amount of litterfall represents the net primary production of forest ecosystems. In ecosystem studies, litterfall measurements have been carried out to estimate the productivity of tropical forests

and litterfall ranges from 5-15 $ton^{-1}ha^{-1}$ $year^{-1}$((Proctor, 1983, Proctor, 1984 , Vitousek & Stanford, 1986, Vogt *et al.,* 1986). Fig. 1 shows the summary of litterfall data in the tropical forests, including the data collected at the Pasoh Forest Reserve in Malaysia and, *Dipterocarpus baudii* plantation at the Forest Research Institute of Malaysia (FRIM). The amount of litterfall in tropical forests are about two times higher than in temperate forests (Vogt *et al.,* 1986, Yamashita *et al.,* 1996). These results show that soil animals are provided with higher amounts of litter for their food and habitat.

The amount of litterfall reflects the productivity of plants, while the decomposition rates of litter represent the decomposer activities. The direct contribution of soil animals to decomposition is minor in comparison with the microbial decomposer and is less than 10 percent of total carbon metabolism of soil sub-systems (MacFadyen, 1971). I have reviewed the decomposition rates of leaf litter and found the decomposition rates were variable depending upon the soil conditions and litter species. The decomposition rates of coniferous needle litter are lower than those of broad-leaved tree species (Takeda *et al.,* 1987).

Fig. 2 summarizes the decomposition rates of leaf litter, including evergreen and deciduous broad-leaved litter in tropical forests. Data decomposition studies at the Pasoh forest, Malaysia is included in this summary. The decomposition rates were studied by a litter bag method and are expressed by the Olson's exponential decay model, $W= W_0 \exp(-rt)$, where W is weight of litter at time t, W_0, the initial weight of litter, t the year, and r the decomposition constant (Olson, 1961). The decomposition rates of leaf litter have been calculated for 51 tree species in tropical forests (Takeda *et al.,* 1984), and 115 tree species in temperate forests (Takeda *et al.,* 1987). The mean decomposition rates are k=1.85 and 0.929 in the tropical and temperate forests respectively (see table 1). The results show that decomposition rates of leaf litter are about two times higher in the tropical than in the temperate forests.

Table 1. A comparison of decomposition rates of leaf litter between the temperate and tropical forest soils. (Decomposition rates are expressed by an exponential model: $W=W_0 \exp(rt)$)

	Decomposition rates	Number of Species
Tropical forests	1.854	51
Temperate forests	0.929	115

THE HABITATS FOR SOIL ANIMALS

Leaf litter is both a habitat and food for soil animals. In tropical forests, two times higher organic matter are supplied for the organization of soil animal communities while the rapid decomposition of leaf litter results in small amounts of litter available for the soil animals. The rapid decomposition rates of leaf litter reflect the accumulation patterns of organic matter on the soils. The amount of forest floor organic matter are shown in Fig. 3. The results showed poorly developed organic layers on the soil surface. Furthermore, the organic layer consists mainly of newly fallen leaf litter, the L layer in tropical forest soils.

So far I have been reviewing the functioning of tropical forest by the amount of litterfall and rates of leaf litter decomposition. Here, the relationships between the

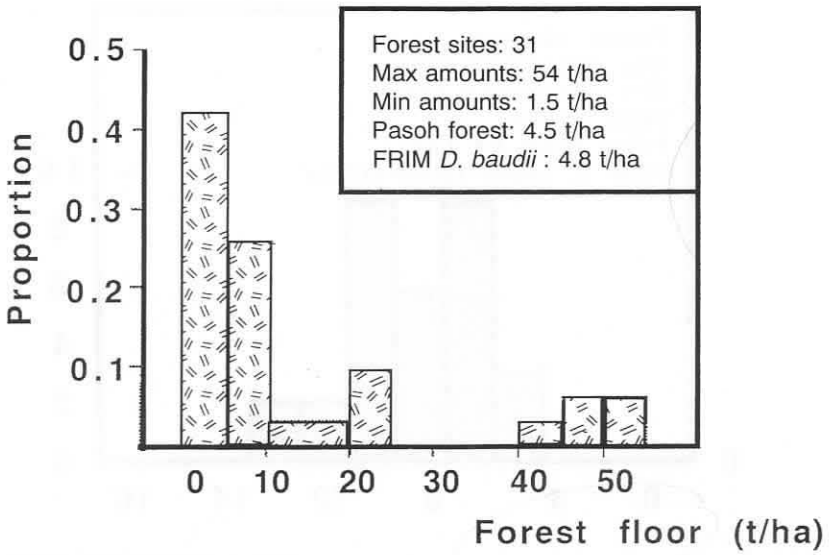

Fig. 1, Data on the amount of litterfall in tropical forests.

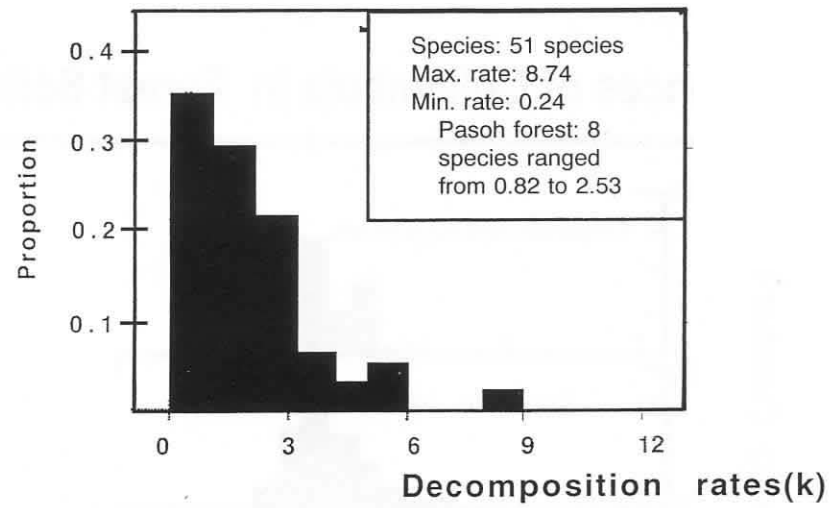

Fig. 2, Decomposition rates of leaf litter in tropical forests. Decomposition studies of 8 species in the Pasoh forests ranged from 0.82 to 2.53. Decomposition rates are expressed by an exponential model.

forest functioning and soil animal abundances are discussed. The general observations have shown that the forest floor of tropical forests support a poorly developed soil fauna. In temperate forest, the mass of the soil organic layer was a major determinant of the carrying capacity of soil microarthropods, such as Collembola and Acari (Takeda, 1987). Based on the compiled data of collembolan abundances of Petersen & Luxton, (1982), population abundances of Collembola are now available for tropical forests, temperate deciduous forests and coniferous forests.

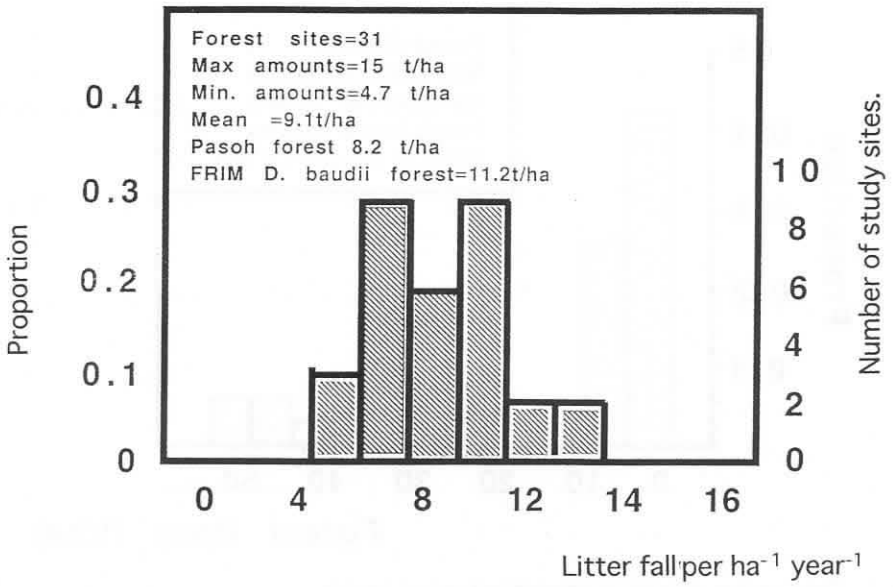

Fig. 3, Amount of soil organic layer in tropical forests. Case studies of the Pasoh and *Dipterocarpus baudii* plantation at the Forest Research Institute of Malaysia are shown.

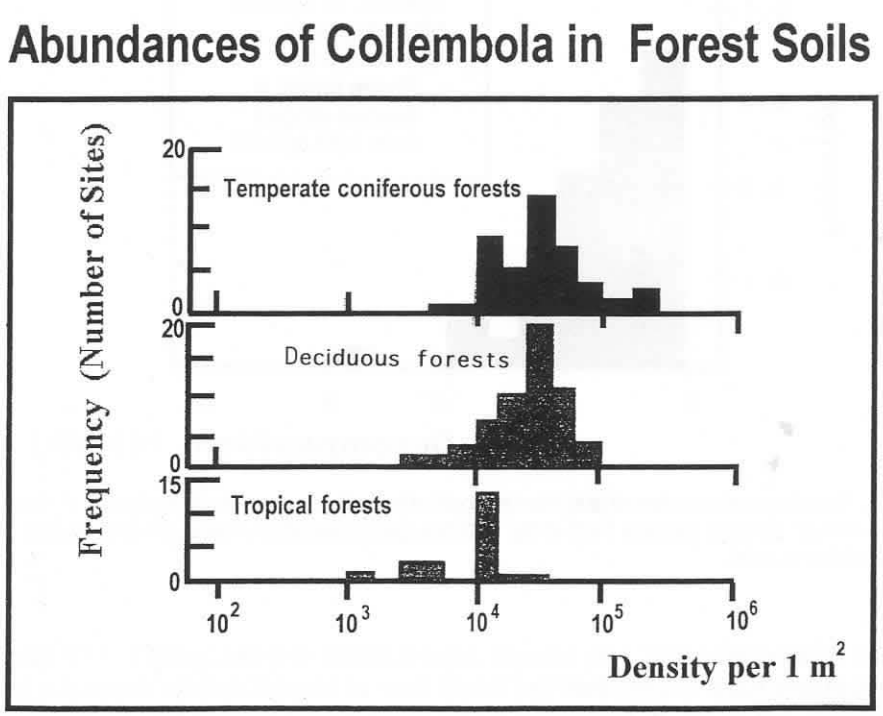

Fig. 4, Abundances of Collembola in temperate coniferous and deciduous forests and tropical forests (Petersen & Luxton, 1982, and Takeda, 1987).

The abundances of collembola range from 10^3 to 10^4 in tropical forests and are one order lower than those of collembola in the temperate forests (Fig. 4). The pooled data suggest that collembolan abundances are determined by the mass of soil organic layer. This implies that the abundances of collembola are predictable throughout the forest functioning, i.e. the amount of litter and decomposition rates of litter in soil layer. The abundances of collembola are determined throughout the activities of primary producers and decomposer microbial populations. Thus, the interactions between the plant-decomposer systems determine the abundances of collembola and probably of other saprotrophic soil animals, such as Acari.

DIVERSITY OF COLLEMBOLAN COMMUNITIES

The soil habitat is characterized by three components i.e., the amount of habitat, the structural complexity, and the micro-habitat associated with the decomposition processes of litter and, the availability of food resources provided through the decomposition processes of litter (Takeda, 1995). In the previous sections, the importance of the amount of habitat is demonstrated. So here I examine the importance of decomposition processes for the organization of soil animal communities, especially for Collembola.

The decomposition processes of leaf litter are briefly described for an understanding of the organization of soil animal communities in tropical and temperate forests. The decomposition processes have been studied in relation to the nutrient dynamics of nitrogen, phosphorus and potassium. Among these nutrients, dynamics of nitrogen have been well studied together with carbon dynamics (Berg and Staaf, 1980, 1981). During the decomposition processes, quality of litter is changed as a result of carbon and nitrogen dynamics by the interaction between heterotrophic microbial and animal populations. Additionally the litter is modified for the colonization of soil animals. The decomposition processes are characterized by leaching and immobilization and mobilization phases of nitrogen and phosphorus. These nutrients often limit microbial populations in soils (Berg & Staaf, 1981). A review of published data in decomposition processes shows that carbon is used by the heterotrophic decomposer with the reservation of nitrogen. So the decomposition progresses with the retention of nitrogen by microbial immobilization until the critical value of carbon to nitrogen ratio(C/N ratio) is seen. From the critical value of C/N about 20, carbon and nitrogen are both mineralized and mineralized from the decomposing litter in the temperate forests (Takeda, 1995b).

Decomposition processes in tropical forests are characterized by the rapid decomposition rates. The decomposition processes are different from those in temperate forests. In the decomposition studies in the Pasoh forest, Malaysia, I studied the decomposition rates of leaf litter of eight tree species including pioneer to climatic species. Initial C/N ratios ranged from 38 to 71 and are comparable with those of temperate tree species. But the nitrogen mineralization commenced at critical values about 23 to 48. The results show that the critical value of nitrogen mineralization is higher in tropical (C/N, 23 to 48) than in temperate forests (C/N about 20). A comparison of decomposition process shows the qualitative differences in decomposition processes between the temperate and tropical forests. The forest soil studies have demonstrated the development of carbon and nutrient sink in organic

and soil layer in the temperate forest (Takeda, 1995c). Temperate forests develop two types of reserve systems of carbon and nutrients. One type has been termed mull humus from where carbon and nitrogen are reserved in mineral soils with a C/N ratio of 10-12, and another type, i.e. mor or moder humus form with a carbon and nitrogen sink of C/N =20. The maintenance of the carbon and nutrient sink is dynamically sustained by nutrient recycling systems of microbial decomposers in the soil. The high critical value of C/N ratio in the decomposition processes in tropical forests suggests a poorly developed recycling systems in tropical soil systems. This result explains why the floor of tropical forests consists mainly of a litter layer. In contrast, temperate forests have thick layers of organic soil consisting of L, F and H layer and mineral soils.

THE FUNCTIONAL GROUPS OF SOIL ANIMALS

Decomposition processes of litter are different between temperate and tropical forests, not only in their rates, but also in the carbon and nitrogen dynamics. The quantitative differences in rates of litter decomposition are the result of differences in abundances of soil animals. Here I show the relationships between the decomposition processes and faunal diversity.

Soil faunal studies in the Pasoh forest showed dominance of termites and ants in the soil arthropod communities. In temperate forests, the majority of soil arthropods are dominated by micro-arthropods, such as Collembola and Acari. Both groups accounted for over 90 percent of the total arthropods in soils. Tropical soils are dominated by social insects such as termites and ants (Abe & Matsumoto, 1979).

The feeding habits of collembolan communities in a pine (temperate) forest, a mixed deciduous forest in Thailand (Takeda, 1981) and a tropical rain forest in Malaysia are analysed. Collembola have been grouped as detritivorous according to their feeding habits. The gut-content analysis of collembolan species showed five feeding groups, 1. fungivorous feeders, 2. saprophagous feeders, 3. carnivorous feeders, 4. sucking feeders and 5. soil feeders (Figs. 5, 6). The tropical forests are characterized by a high diversity of fungivorous collembolan species and, low abundances of saprophagous species. The fungivorous species are represented by members of the genus *Lepidocyrtid* collembolan spp. There are few species in this genus in temperate forests, but this group of collembolans is highly diverse in tropical forests (Yoshii, 1982). Feeding groups of collembola are related to the decomposition processes in soils. In the temperate systems, saprophagous collembola such as Onychiurid and Isotomid collembolan species, are abundant and diverse because of the recycling systems in the soils. In contrast, the saprophagous species are poorly represented in tropical forests with poorly developed recycling systems. So, in the tropical systems, the fungivorous species may be advantageous in their grazing abilities and species diversity.

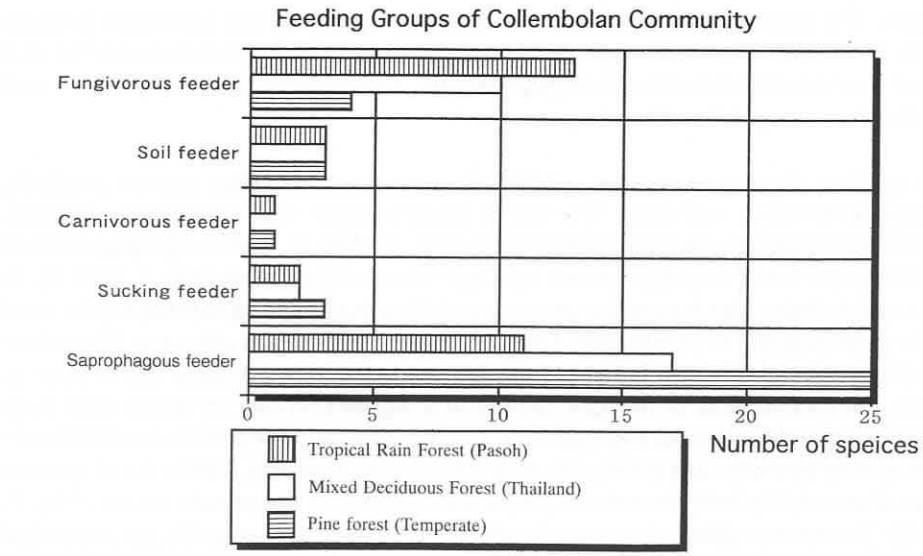

Fig. 5, Types of feeding groups in tropical rainforest, mixed deciduous and temperate forest collembolan communities. Collembolan species are grouped into five feeding groups.

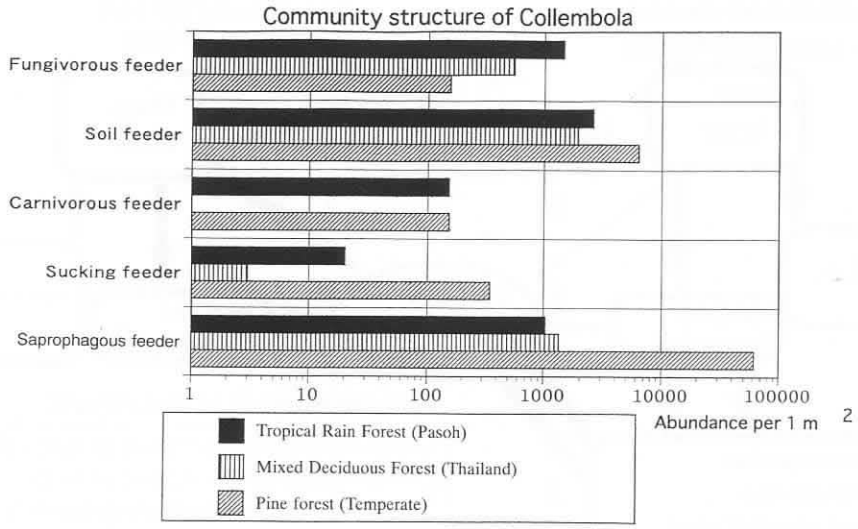

Fig. 6, Community structure of Collembolan tropical rainforest, mixed deciduous and temperate forest. Collembolan species are categorised into five feeding groups and abundances of each group are shown.

CONCLUSION

Fig. 7 shows the decomposer systems in the temperate and tropical forests. The functioning and structure of terrestrial ecosystems are shaped and maintained by the plant-decomposer interactions. The food and habitat of animal populations are biogenic and mainly of plant origin (plant litter) in terrestrial ecosystems. In soil sub-

systems, the food-habitat templates are provided mainly by the plant litter such as leaves, branches and fallen logs. Plant litter is used by microbial populations and carbon is mineralized by microbial populations. Soil animals are poorly developed to utilize the newly fallen litter.

After the loss of tannin and other inhibitor through leaching, litter may be available as food for termites and ants. The social insects might have competitive abilities with the decomposer microbial populations (Fig. 7, Path 1). The fungal populations that colonized the litter may be used by fungivorous soil animals (Fig. 7, Path 2). In temperate forests, decomposition processes follow the leaching, immobilization and mobilization processes of nitrogen. The mobilization of nitrogen occurs at the carbon and nitrogen ratios of about 20 in organic soil and 12 in mineral soils. But in tropical forests, the mobilization of nitrogen occurs at a higher C/N ratio of about 35 in soils with poorly developed recycling systems. So, the detritivous feeder depending upon the recycling systems are poorly developed in tropical forests. While these groups are predominant in their abundances and diversity in the temperate forests (Fig. 7, Path 3). The composition of various functional groups of soil animals are explained by the decomposition processes in both the forests. The present study provides some clues to the understanding of the diversity of soil animals through the interactions of plant-decomposer systems in forest ecosystems.

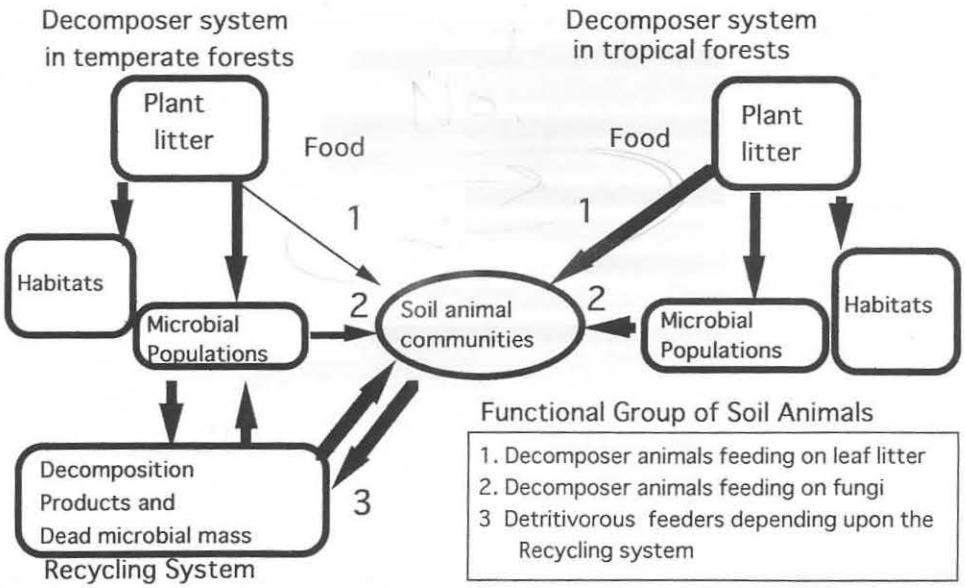

Fig. 7, A model of soil animal communities and decomposition systems in temperate and tropical forests. Soil animals are categorised into three functional groups based on feeding habits. In tropical forests, detritivorous feeders are very poorly represented in comparison with those in the temperate forests.

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